Hydrological niches in terrestrial plant communities: a review

ESSAY REVIEW

Hydrological niches in terrestrial plant communities: A review

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Summary

1. Despite the fundamental significance of water to plants and the persisting question of how competing species coexist, this is the first review of hydrological niches. We define hydrological niche segregation (HNS) as: (i) partitioning of space on fine-scale soil-moisture gradients, (ii) partitioning of water as a resource, and/or (iii) partitioning of recruitment opportunities among years caused by species specializing on particular patterns of temporal variance of water supply (the storage effect).

2. We propose that there are three types of constraint that lead to the trade-offs that underlie HNS. (i) An edaphic constraint creates a trade-off between the supply to roots of O_2 on the one hand vs. water and nutrients on the other. (ii) A biophysical constraint governs gas exchange by leaves, leading to a trade-off between CO_2 acquisition vs. water loss. (iii) A structural constraint arising from the physics of water-conducting tissues leads to a safety vs. efficiency trade-off.

3. Significant HNS was found in 43/48 field studies across vegetation types ranging from arid to wet, though its role in coexistence remains to be proven in most cases. Temporal partitioning promotes coexistence through the storage effect in arid plant communities, but has yet to be shown elsewhere. In only a few cases is it possible to unequivocally link HNS to a particular trade-off.

5. *Synthesis.* The field and experimental evidence make it clear that HNS is widespread, though it is less clear what its precise mechanisms or consequences are. HNS mechanisms should be revealed by further study of the constraints and trade-offs that govern how plants obtain and use water and HNS can be mechanistically linked

to its consequences with appropriate community models. In a changing climate, such an integrated programme would pay dividends for global change research.

Key-words: coexistence, eco-hydrology, global change, hydrological niche, plant community ecology, plant population and community dynamics, stable isotopes

Introduction

Terrestrial plants use water for just about every function imaginable. It is used structurally to provide cell turgor, as a raw material, a solvent, a transport medium and a coolant. Transpiration of water is the source of motive power in the xylem and the photolysis of water provides hydrogen atoms for the biosynthetic reactions of photosynthesis. Plants also require a flux of water in order to take up nutrients. Water is so obviously essential to physiological functions that it is arguable that ecologists have overlooked the more subtle importance of water to plant community structure, except in habitats where it is clearly in short supply. Part of the reason for this oversight must be that water, like light, O_2, CO_2 and the major nutrients N, P and K, is an essential resource for all plants and there just don't seem to be enough ways for species to partition these into the hundreds of niches required for stable coexistence in the most species-rich plant communities (Silvertown 2004).

The problem of coexistence in plant communities and its potential solutions have been recently reviewed by Wilson (2011). The idea embodied in neutral theory that niches are unnecessary or irrelevant to plant coexistence (Hubbell 2001), looks increasingly untenable in the light of recent studies (Levine & HilleRisLambers 2009; Adler *et al.* 2010; Clark 2010; Purves & Turnbull 2010) . It is therefore timely to ask how important hydrological niches might be to plant community structure, particularly since hydrology is expected to be altered by climate change and therefore this information is of practical, predictive value (Bartholomeus *et al*. 2011; Strom *et al.* 2012).

Fan *et al.*(2013) estimate that the water table lies near to the surface in nearly a third of the Earth's land area, indicating the global importance of groundwater hydrology to plant communities, but hydrological niches are not confined to such areas. The evidence is growing that across the full range of water availability from arid habitats to wetlands (Webb *et al.* 2012), even closely related species differ in their tolerance of water deficit or excess and how these conditions vary over time (Parolin *et al.* 2010; West *et al.* 2012; Craine *et al.* 2013). These differences among species frequently manifest themselves in the segregated distribution of species along gradients.

For the purposes of this review, terrestrial plant communities include 'wetlands' that may be temporarily flooded, but not those that are fully aquatic. The physical scale of the soil-moisture gradient affecting plant community composition may range from the geographical to the highly local. Moeslund *et al*. (2013b) surveyed vegetation composition and variation at spatial resolutions from 2 m–250 m across 43,000 km^2 in Denmark. They found that topographically-related soil wetness was the primary determinant of habitat type. The same variable determined variation among grassland habitat types (Moeslund *et al.* 2013a). Also working at a geographic scale, Schietti *et al.* (2014) found that 82% of the variance in plant composition among plots in Amazon terra firme forest could be accounted for by the depth to water table.

In temperate forest in France, soil-water balance was a better predictor of tree species distribution than Potential Evapotranspiration (PET) derived from climatic variables (Piedallu *et al.* 2013). This result underlines the point that plants react to local soil moisture availability and that this must ultimately be responsible for their segregation on gradients at large, as well as fine, physical scales. For this reason, the soil-moisture responses of species can be expected to show correlations across spatial scales. Such a

correlation between drought tolerance and distribution at geographic and more local scales is commonly found among tropical tree species (Comita & Engelbrecht 2013).

In this review, we focus mainly on the fine spatial scale relevant to α-diversity and the α-niche because it is fundamental both to coexistence (Silvertown 2004) and to processes determining distribution at larger scales. Following Araya *et al*. (2011), we define hydrological niche segregation (HNS) as "(i) partitioning of space on fine-scale soil-moisture gradients (fine-scale being defined as a distance sufficiently small for species to compete for the same resources), or (ii) partitioning of water as a resource through different strategies of water acquisition such as different phenologies or different rooting depths." To this pair of definitions we now add a third that logically belongs with them, which is (iii) partitioning of recruitment opportunities among years caused by species specializing on particular patterns of temporal variance of water supply. This can promote coexistence through the temporal storage effect (Chesson *et al.* 2004).

In this review, we firstly consider the theoretical requirements for hydrological niche segregation, then we survey the field evidence for the existence of HNS within communities and finally we discuss these field-survey results in the light of experimental and other evidence.

Hydrological niche segregation

Coexistence mechanisms

Chesson (2000) distinguished between coexistence mechanisms that equalize interspecific competitive abilities, for example as in the neutral model (Hubbell 2001), and those that stabilize communities through frequency dependence. The

essential condition for a mechanism to be stabilizing is that it should cause any species to increase when rare. A community of two competing species can satisfy this condition if each is limited more by intraspecific competition than by interspecific competition. Niche segregation has this effect because as population density increases, the impact of intraspecific competition rises and the impact of interspecific competition falls, thus relieving rare species from competitive pressure by other species.

The temporal instability of soil moisture, which can be very variable from year to year (Terradas *et al.* 2009), is a feature of hydrological niches not shared by other resource gradients such as light or nutrients that tend to change gradually. Seedlings are typically more vulnerable to drought than are mature plants with deeper roots and hence plants may have different strategies of survival in the regeneration and the later phases of the life cycle (Grubb 1977). This decoupling between the conditions required for recruitment, for example through the release of seeds from dormancy, and for adult survival is a pre-condition for the temporal storage effect. Established plants (or seeds) that are resistant to drought are "stored" over periods that are too dry for seedling recruitment.

The temporal storage effect in which species depend for recruitment on different patterns of temporal variance in water availability, needs to be distinguished from other hydrological niche dimensions with which it is likely to be correlated such as the amount or the depth of the water resource. For example, temporary water bodies such as vernal pools often have their own specialized flora of ephemeral species (Deil, 2005) and while it is clear that these communities occupy a β (habitat) niche that is characterized by a fluctuating water supply, it is less clear whether the coexistence of

120 species within the pool also depends upon fluctuation. The species are typically zoned
121 from the pool margin to its interior so the zone of a species defines its α niche, but in
122 any particular zone the amount of soil water, the duration of the drought as the pool
123 dries up, the depth of water and the duration of inundation are all correlated so it is
124 impossible to tell without experimental manipulation whether the pattern of temporal
125 variance *per se* is an important dimension of the α niche.

126 Nygaard & Ejrnaes (2009) factorially manipulated nutrients, water-table depth and
127 degree of water-level variance in mesocosms sown with a standard mixture of 23
128 wetland species. Both nutrient and water-level treatments influenced the resulting
129 community, with the infertile, dry treatment containing the largest number of species.
130 However, water-level variance had no main or interactive effect on the plant
131 community, implying the absence of temporal niche separation.

132 The presence of niche differences between species is not in itself sufficient evidence
133 that niche segregation is the actual mechanism of coexistence (Silvertown, 2004), but
134 it is a necessary first step towards testing whether this is the case. Confirmation
135 requires either experimental manipulation of resources to demonstrate that
136 coexistence depends upon the presence of niche differences, or parameterization of
137 community models that can then be manipulated to determine which processes
138 stabilize community composition (Rees *et al.* 1996; Silvertown & Wilson 2000;
139 Groeneveld *et al.* 2002; Levine & HilleRisLambers 2009).

140 ## Trade-offs

141 Niche segregation arises when trade-offs force species to specialize in the zone of
142 niche space where they grow best (Chase & Leibold 2003). Silvertown *et al.* (1999)

143 demonstrated a trade-off between species' tolerances of aeration stress and tolerances
144 of soil drying stress in English meadows where the presence of HNS was supported
145 by field data. An identical pattern was later discovered in fynbos habitats, strongly
146 suggesting that the trade-off in question is fundamental and arises from compromises
147 inherent in the physiology of plant water relations (Araya et al., 2011). In Sonoran
148 desert annuals, Angert *et al*. (2009) found that coexistence depended on a trade-off
149 among species between water-use efficiency and relative growth rate.

150 We propose that there are three overlapping types of physiological constraint that
151 contribute to the overall pattern of trade-offs, none of them mutually exclusive (Fig.
152 1).

153 Fig.1. here

154 First is the edaphic constraint that is imposed by the soil environment and which
155 affects the supply of O_2, water and nutrients to roots. This derives from the fact that
156 soil-pore space may contain water (and dissolved nutrients) or air, but if pores are
157 predominantly filled by water, plants' roots may be deprived of oxygen and if
158 predominantly filled by air, they may be deprived of water and nutrients. This edaphic
159 constraint presumably explains why below-ground competition is so important to
160 hydrological niche segregation (Bartelheimer *et al.* 2010; Silvertown *et al.* 2012).

161 The interactive effects of water and nitrogen in soil were neatly shown in a mescosm
162 experiment by Nygaard & Ejrnaes (2009). The response of individual species to
163 water regime in this experiment was strongly influenced by nutrient availability and
164 overall species richness was determined primarily by the interactive effects of the
165 water and nutrient treatments. Araya *et al.* (2012a) demonstrated a direct mechanism

by which water-regime controlled nitrogen availability, thereby revealing how water-regime can control RGR even when water is itself a non-limiting resource.

Both intrinsic water-use efficiency (WUE: the amount of carbon fixed per unit of water consumed) and nitrogen-use efficiency (NUE; the amount of carbon fixed per unit of nitrogen taken up) are highly phenotypically plastic and exhibit a trade-off at the leaf-level (Patterson *et al.* 1997). A WUE/NUE trade-off has also been found at species-level in trees and shrubs (Field *et al.* 1983) and grasses (Chen *et al.* 2005; Gong *et al.* 2011) where differences in species' relative performance on the trade-off correlate with their distribution on soil moisture and nutrient gradients. The cause of the WUE/NUE trade-off may be the dependence of nutrient acquisition on water uptake.

Second is the biophysical constraint that governs gas exchange by leaves. This arises from the fact that stomata regulate both CO_2 acquisition and loss of water through transpiration. Other things being equal, the biophysical constraint means that closing stomata to limit water loss incurs a cost in CO_2 uptake. This constraint is inherent in the equation for intrinsic water use efficiency, $W_g = A/g_s$ which is the ratio of net assimilation *(A*) of CO_2 to the stomatal conductance of water (g_s) (Seibt *et al.* 2008). In drought, plants commonly increase W_g by closing stomata (decreasing g_s), but the degree to which this happens varies both between (Cernusak *et al.* 2007) and within species (Edwards *et al.* 2012). We propose that this variation provides the biophysical basis for hydrological niche segregation at the drier end of the soil-moisture gradient where plants must conserve water (Moreno-Gutierrez *et al.* 2012). Heritable variation in W_g, which is typically high, is potentially the basis for ecological speciation. Koziol *et al.* (2012) found that selection during the domestication of sunflowers resulted in a

decrease in drought tolerance and an increase in growth rate as a result of a trade-off between these traits.

Third is the structural constraint that arises from the physics of water-conducting tissues. The rate at which water moves through a plant is often the determinant of its gas-exchange rate, its photosynthetic rate and thus its relative growth rate (RGR) (Zimmerman 1983). To compete effectively with its neighbours, it may therefore be important for a plant to maximise its transpirational flux through its xylem system. High water fluxes require either steep gradients in water potential and/or wide xylem vessels with high hydraulic conductivity, both of which increase the risk of embolism (Sperry & Tyree 1988). Given this understanding, specialised xylem structure has long been postulated as another possible trade-off with respect to water economy. The topic was being discussed as far back as 1918 (Bailey & Tupper 1918) and its development has been neatly reviewed by (Tyree *et al.* 1994), who undertook a meta-analysis of twenty earlier studies to demonstrate a trade-off between hydraulic efficiency and safety existed. Smaller xylem conduits especially those characterised by thicker walls, fewer pits and specialized pit membranes (Lens *et al.* 2013) can tolerate low water potentials without embolizing, giving the plant a margin of safety when conducting water up to its leaves at close to its maximal rate, even if the atmosphere is very dry (Manzoni *et al*, 2013). Larger vessels on the other hand provide longer, wider conduits with more pits or complete perforations in their walls. These provide higher hydraulic conductivity and therefore greater efficiency, allowing them to conduct an equivalent amount of water without requiring such a steep gradient. However, they are at greater risk of cavitation at a given water potential.

This safety versus efficiency trade-off is discussed by Manzoni (2013), who demonstrated that trees operate at close to their maximum rates of transpiration, and thus are frequently prone to embolism. The authors showed that maximal rates of transpiration were relatively constant within a given environment, but the means by which species achieved them could differ greatly. Some, notably those that tolerate harsh conditions (e.g. many coniferous trees) use fine conducting elements (tracheids), which deliver a low efficiency of water transmission, but provide a high resistance to failure. Deciduous angiosperm trees in contrast tend to produce larger xylem elements (vessels) that provide higher efficiency of water transport when water potentials are high, but which are more vulnerable to cavitation when water potentials fall (Maherali *et al.* 2004). However, these angiosperms appear able to operate at closer to the their maximum transpiration rates because they also display a greater ability to repair cavitated vessels (Johnson *et al.* 2012). Water-conducting tissues in trees have been shown to operate at close to their embolism threshold across all biomes, with angiosperms generally displaying a narrower safety margin than gymnosperms (Choat *et al.* 2012).

This safety versus efficiency trade-off has been linked to species-distribution patterns in forest. Markesteijn *et al.* (2011) postulated that species' hydraulic architecture would be a major driver of their partitioning along soil-moisture gradients. They measured hydraulic traits in 40 species in a stand of tropical dry forest and found large differences among species and a strong trade-off between efficiency and safety. They clearly showed the trait that best characterized trees in resource poor areas (whether shaded or dry) was high density of wood (i.e. small xylem element size), as described above, and concluded that hydraulic capacity is integrally linked to niche differentiation.

The field evidence for hydrological niche segregation

We conducted a survey of the literature on the use of water by coexisting plant species in the field using the Web of Knowledge to identify papers that cited foundational studies by Davis & Mooney (1986), Manning & Barbour (1988), Ehleringer *et al*. (1991) and Silvertown *et al*. (1999). All papers cited by the citing papers were then evaluated and so on iteratively until no new studies of relevance were found. This search was limited to papers published before March 2013 and we identified 48 studies in which water utilization or distribution on soil-moisture gradients had been statistically compared for at least two coexisting species. The modal species number per study was only 3 (10 studies) and the median was 5 species. These numbers are low, but many of the species studied were actually the dominants in their communities and therefore the differences in their hydrological niches are of particular significance.

The 48 studies have been grouped according to the three mechanisms of hydrological niche segregation mentioned in the introduction. Studies of species growing on a soil-moisture gradient are summarized in Table 1 (studies #1 - #11), those where partitioning of water as a resource was tested are shown in Table 2 (studies #12 - #43) and tests of the temporal storage effect are grouped in Table 3 (studies #44 - #48).

Studies are ranked within each table by the average annual amount of precipitation occurring at the study site. We recognize that this ignores variation in evapotranspiration rates and also groundwater as a source, but these limitations do not obscure the fact shown by the data that plants segregate on hydrological gradients in a remarkably wide range of terrestrial environments ranging from arid to wet. Forty-three of the 48 studies listed reported evidence of significant HNS. An attempt was

made to cross-classify the three groups of studies by the three trade-off types in Fig.1., but very few of the source papers contained enough relevant information to make this possible. Those where clear trade-offs have been demonstrated are singled out for mention below.

Species growing on a soil-moisture gradient

Table 1 here

Although only 11 instances of such studies were found by our search methodology (Table 1), there is a mostly older literature containing many similar cases (Rutter 1955; Boedeltje & Bakker 1980; Grootjans *et al.* 1988; Wierda *et al.* 1997; Kotowski *et al.* 1998). Three field experiments are included in Table 1. Reynolds *et al.* (1997) reciprocally transplanted 3 annuals that occupied soil patches with different soil water content, finding that each did better on its home patch. In an experiment that altered soil moisture in a perennial grassland community on shallow limestone soil, Fridley *et al.* (2011) (#11) found that 13 of the 25 species investigated showed soil-depth affinities and that the majority of these moved along the soil-depth gradient in response to climate change treatments that directly or indirectly changed soil moisture.

Another experiment on a community where species segregated on parallel gradients of soil depth and soil-moisture content showed that soil moisture was the driving variable in the segregation of the two competing annuals *Sedum smallii* and *Minuartia uniflora* that occupy zones of different soil depth in depressions in granite outcrops (#10). Clear examples are reported of biophysical trade-offs in a mediterranean shrubland (#2) and of edaphic trade-offs in fynbos (#3) and floodplain meadows (#8)

(Table 1). A structural trade-off may be the basis of different drought tolerances and coexistence in two species of *Adenostoma* in S.California (#4).

Water partitioning among species

Table 2 here

The majority of studies (32/48) surveyed fell into this category (Table 2). Most were descriptive rather than experimental in approach and used stable isotopes to compare the different sources from which co-occurring species drew their water. Twenty-eight studies out of 32 found significant evidence of HNS, but there was negative evidence in five cases (#24, 29,30,31, 36, Table 2). In two of them (#29, 30), sampling was conducted at a time of year when water might be expected to be least limiting. Liu *et al.*(2011) conducted their study comparing two subalpine shrubs in Sichuan, China during the monsoon season (#29). In a study of savanna shrubs in Texas (#30), stable isotopes sampled during the season of greatest rainfall showed no differences among species in the depth of water sources utilized, although rooting depth profiles were different. In another study of two evergreen savanna trees *Quercus fusiformis* and *Juniperus ashei* growing in a karst region in Texas (#31), the species also had indistinguishable isotopic signatures of water source during and after drought. However, these species are known to have different water-use strategies, with needle-leaved *J. ashei* able to tolerate drought and sustain gas exchange during water shortage while broad-leaved *Q. fusiformis* does not and a recent study found that there is a phenological dimension to HNS between these species (Kukowski et al., 2013).

Five studies compared overlap in use of water sources over more than one season. In three studies the overlap was least in the season of greatest scarcity (#13, 17, 32,

Table 2), as would be expected if HNS is driven by resource competition for water when it is most limiting. In another study, Verheyen *et al.* (2008) (#27) found that total evapotranspiration was greater in mixtures of species than in the best performing monocultures, providing evidence of niche complementarity for water use under normal conditions. This effect disappeared in conditions of drought. The fifth study (#33) also found that, in three subalpine woody plants, species that utilized different water sources when rainfall was available were constrained to all use the same source in dry conditions. The critical issue required to interpret all these results is how relative population growth rates among the coexisting species are affected by water availability (Verhulst et al., 2008). If most or all species cease growth in drought, then it is HNS at times of greater water availability that is important to coexistence and not how species use water when it is most scarce. Drought-induced mortality may still differ between species of course.

Trade-offs were investigated surprisingly rarely among these studies, given how large the sample was. From the evidence of structural trade-offs among tropical trees already discussed (Markesteijn *et al.* 2011), one might guess that they underlie the differentiation among tree species in rooting depth (#42) and degree of dry-season deciduousness (#43) found in seasonally dry forest at Barro Colorado in Panama.

Temporal storage effect

Table 3

Although only five studies were found in this category, three of them demonstrated that the temporal storage effect promoted coexistence. In a community of Sonoran Desert annuals, Angert *et al*. (2009) (#45) found that the decoupling of reproductive

success between species that is required by the temporal storage effect was in part caused by the biophysical trade-off between relative growth rate (RGR) and intrinsic water use efficiency (WUE). Species with low RGR and high WUE were able to exploit small, but frequent rainfall events, while species with high RGR and low WUE did best under large, infrequent rainfall events. Temporal niche separation caused by different responses to the size of variable rainfall events was also found between two desert shrubs in the Chihuahua desert (Verhulst *et al.* 2008) (#46), and among three dominant prairie grasses in Kansas (Adler et al., 2006) (#48). In both of these cases models demonstrated that the temporal niche differences that were observed did actually promote coexistence. The two remaining studies in Table 3 found that species of steppe communities in Patagonia (#44) and N.W. China (#47) differed in their response to rainfall in a fashion that would suggest temporal niche segregation, although the effect of this on coexistence was not tested.

Discussion

This is the first review of hydrological niches in plant communities and it has revealed that niche segregation is widespread, occurring in at least 43 out of the 48 studies examined. It is possible that our survey methodology contained a bias in favour of finding positive results, but this would not alter the conclusion that HNS has been found in vegetation types ranging from arid to wet environments and from arctic alpine to tropical forest.

We divided the 48 cases into three groups, depending upon whether the niche segregation investigated was on a soil moisture gradient (i.e. spatial) (Table 1), involved partitioning of water resources by, for example, different rooting depths (Table 2), or tested temporal differences between species (Table 3). Very unequal

numbers of studies fell into the three categories, but we attach little biological significance to this because sample sizes are influenced to an unknown degree by sampling error and the cost and availability of methods for investigating different mechanisms. For example, measuring water partitioning using stable isotopes has become routine and inexpensive (Dawson *et al.* 2002) (Table 2, n = 32), compared to the labour-intensive, long-term surveys that are required to evaluate spatial (Araya et al., 2011) (Table 1, n = 11), or temporal (Angert et al., 2007) (Table 3, n = 5) HNS.

One clear pattern that may be of biological significance is the predominance of arid communities among the studies of the temporal storage effect (Table 3). All five studies were of communities with low precipitation values that lay below the median for the sample as a whole 588 mm (n = 48). All the studies demonstrated temporal HNS and three of the five showed that this was sufficient to promote coexistence. Is the temporal storage effect confined to arid communities? It is too early to say, but we believe that there is no reason why it should be. Flooding, as well as rainfall, can be very variable from year-to-year and there is ample evidence among the studies in Table 1 and elsewhere that plants differ in how they respond to this. To our knowledge, the storage effect has not yet been tested in plant communities subject to flooding, but this is an area ripe for investigation.

The majority of the field studies surveyed were observational, but 11 of the 43 studies where HNS was found involved field experiments that manipulated soil moisture and/or plant-plant interactions. The mechanisms generating HNS require further field investigation, but mesocosm experiments have implicated the importance of soil nutrient availability, soil microbial composition, oxygen availability, water deficit and interspecific competition below-ground. The experimental investigation of

hydrological niches began with the now classic lysimeter experiments performed by Heinz Ellenberg in the 1950s (Ellenberg 1953; Hector *et al.* 2012) in which he grew meadow grasses in monocultures and in mixtures along a soil-moisture gradient created by a gradient of soil depth. There was an almost complete overlap of the fundamental niches among the six monocultures (94%), but a much reduced overlap of realized niches in conditions of interspecific competition (72%). Although there was still substantial overlap of hydrological niches in the mixture, the reduction of 22% caused by interspecific competition was highly significant ($P < 0.001$) (Silvertown *et al.* 1999).

Ellenberg's experiment was a powerful, early investigation of the existence of hydrological niches among meadow grasses. However, the experimental design used in the 1950s was unreplicated and did not take account of possible spatial autocorrelation along the gradient or the covariation of water-table depth with soil volume. All these limitations can be overcome by the use of mesocosms, which are soil containers that permit the independent, replicated manipulation of water-table depth and other variables for plants growing in an outdoor environment (Araya *et al.* 2010).

In a mesocosm competition experiment with two species of *Senecio*, one native to wet- and the other to dry grassland, Bartelheimer *et al.* (2010) found that below ground interspecific competition with the roots of grasses was responsible for limiting the growth of the dry-habitat species in wet conditions, where without root competition it could grow quite successfully. A meta-analysis of 38 experiments found that this may be a common phenomenon, with competition below ground often

more important than competition above, especially in competition with grasses and in conditions of low fertility (Kiær *et al.* 2013).

Using mesocosms, Vivian-Smith (1997) demonstrated the importance of microtopography, showing that segregation occurred among wetland species establishing from seed on hummocks and hollows that were only 10–30 mm different in height. Soil-moisture content, air-filled pore space and nitrogen availability are all greatly influenced by the depth of the water table beneath the soil surface and any or all three could be responsible for the observed effect of microtopography.

Water displaces air from soil pores, reducing oxygen availability and altering the composition of the microbial community, which also segregates on soil-moisture gradients (Wolfe *et al.* 2006; Cavender-Bares *et al.* 2009; Araya *et al.* 2012a; Lennon *et al.* 2012). Nitrification in soil depends upon an aerobic microbial community, whilst nitrate ions are consumed by an anaerobic community, so waterlogged soils are low in plant-available nitrogen as well as in oxygen (Patrick & Wyatt 1964). Though the availabilities of water, oxygen and nitrogen covary, they can be decoupled experimentally to determine the relationships among the variables. Araya *et al.* (2012a) manipulated air-filled pore space independently of soil-water content and found that nitrogen mineralization was greatly inhibited at values of air-filled pore space less than 10%. The same effect is seen when soil-water content reduces air-filled pore space below this percentage. In the field, nitrogen-mineralization rate showed an optimum at 40 cm water-table depth, decreasing either side of this value when at shallower depths there was an oxygen deficit and at deeper levels water deficit limited microbial decomposition. The absolute value of the optimum depth is

likely to vary widely according to the pore-size distribution and microbial respiration rate of the soil.

The combination of field and experimental evidence that we have assembled in this review paints a picture of a field that is ripe for synthesis, but that at present lacks some important components. We believe that it is clear that HNS is widespread, but less clear what the precise mechanisms or their consequences are. The starting point for uncovering HNS mechanisms should be the study of the constraints and trade-offs that govern how plants obtain and use water. The three constraints that we identified (Fig.1) are unlikely to be the only ones operating, but the field evidence at present is frustratingly sparse.

The consequences of HNS also need further investigation. In a few cases already mentioned it is clear that HNS is responsible for coexistence and in a larger number we can at least say that HNS influences community assembly. More studies need to use appropriate community models so that HNS can be mechanistically linked to its consequences. This is important not least because improving our understanding of hydrological niches is needed to predict the consequences of environmental change.

Global warming is expected to increase the variability of precipitation patterns (Allan & Soden 2008) which is likely to have a greater impact on the composition of vegetation communities than the change in temperature regime itself (Reyer *et al.* 2013). Many plant species have such wide latitudinal ranges and exhibit such a broad tolerance of temperature regime that the climatic envelope approach is unlikely to be able to resolve future distributions at anything finer than a regional scale (Zelazowski *et al.* 2011). In contrast, the sensitivity of species in terms of their preferred hydrological niche is acute (Silvertown *et al.* 1999) and plants are phenotypically

449 plastic in response to changes in soil moisture (von Arx *et al.* 2012) as well as stresses
450 such as flooding (Bailey-Serres & Voesenek 2008).

451 Bartholomeus *et al.* (2011) modelled the effects of future climate scenarios on the
452 stresses (both drought and aeration) that grassland plants could be exposed to in
453 future. Their conclusions were that due to increased variability in precipitation, the
454 main impact would be an expansion in the number of sites that experience a
455 combination of both stresses in different seasons of the year. They showed that rare
456 species of conservation importance tend to be absent from such sites and therefore it
457 is this group that would be disproportionately affected by climate-change in the
458 future. They emphasise the point that in order to predict vegetation change, you need
459 to consider the soil moisture regime in detail, because the interaction of the two
460 stresses (lack of soil oxygen and lack of soil water) cannot be easily generalized.

461 Implicit in their argument is the need to characterize the realized hydrological niche
462 of each species and to build process-based models. Such models now exist for the
463 Netherlands (Witte *et al.* 2012) and are emerging elsewhere (Robinson *et al.* 2008;
464 Seneviratne *et al.* 2010; Maclean *et al.* 2012; Orellana *et al.* 2012). However, there is
465 much still to do. Methods in eco-hydrology are not standardized, even for recording
466 variables as basic as the effects on vegetation of manipulating precipitation (Vicca *et*
467 *al.* 2012). Cross-correlation is needed between the stable isotope methods used to
468 measure water use by so many studies and direct measurements of plant-available
469 water. The accumulating evidence for hydrological niches in plants now shows that
470 the field merits the attention of an integrated programme linked to global change
471 research.

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Tables

Table 1

Table 1. Studies of hydrological niche segregation through the partitioning of space on fine-scale soilmoisture gradients. Any differences among species are those found to be statistically significant in the original studies

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
1	Alpine tundra	Alberta, Canada	~25	3 *Salix* spp.	Species occupied distinct though overlapping zones along a topographic and soil moisture gradient. Species position on the gradient correlated with physiological measures of water relations, indicating the likely role of HNS.	(Dawson 1990)
2	Mediterranean shrubland	Spain	288	1 grass and 9 coexisting shrub species of various size	Based upon stable isotope analysis, the ten species segregated along a gradient of water use characteristics from low stomatal conductance (g_s) and high WUE to high g_s and low WUE. The ranking of	(Moreno-Gutierrez *et al.* 2012)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
					species on the gradient was unaffected by differences in rainfall between years.	
3	Fynbos	Western Cape, South Africa	350 - 1400	Restionaceae and fynbos community as a whole separately analysed	Distributions in SEV niche space tested against null models showed HNS among Restionaceae in 7 of 10 sites and for the entire community in 9 out of 10 sites.	(Araya *et al.* 2011, 2012b)
4	chaparral	S.California, USA	403	2 co-occurring shrubs *Adenostoma fasciculatum* and *A. sparsifolium*	*A. sparsifolium* had much deeper roots than *A. fasciculatum* but the latter species was more resistant to xylem embolism caused by water stress than the former. Redtfeldt & Davis(1996) made this comparison between adjacent plants, but Beatty (1987) found that the species usually occupied different microsites and were only rarely found as nearest neighbours.	(Beatty 1987), (Redtfeldt & Davis 1996)
5	Temperate swamp forest	Budějovická, Czech Republic	575	3 mosses, 11 perennial herbs, a fern, a floating	Distribution of 9 of 17 species varied significantly across a water table depth gradient of about a metre in vertical	(Douda *et al.* 2012)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				aquatic and a tree	range.	
6	serpentine annuals	California, USA	589	3 annuals *Calycadenia multiglandulosum, Plantago erecta,* and *Lasthenia californica*	Soil water content varied among patches dominated by the 3 different species. A reciprocal sowing experiment among patches showed a home-site advantage for all 3 species.	(Reynolds *et al.* 1997)
7	riparian meadow	Oregon, USA	650	18 species of sedge, rush, grass and forb	Median water table depths varied among the 18 species over a 50cm range, but with widely overlapping ranges.	(Dwire *et al.* 2006)
8	floodplain meadow	England, UK	680	2 communities containing 83 species of herbaceous meadow plants	Community-wide segregation found in niche space defined by axes of SEVa and SEVd in both communities.	(Silvertown *et al.* 1999)
9	mire	SE Norway	800	24 species including 9 vascular plants, 5	Along a water table gradient of 0–25cm depth, all 24 species exhibited some degree of 'preference' for a particular	(Nordbakken 1996)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				Sphagnum spp., 6 hepatics and 4 lichens	depth to water table (DWT). The full range of preferences (0–25cm median DWT) was found among the 9 vascular plant species, with species in each of the other 3 groups showing medians between 0–15cm DWT.	
10	rock outcrop	Georgia, USA	~1,000	Annuals *Sedum smallii* and *Minuartia uniflora*	Coexisting annuals shown experimentally to partition the rock depressions in which they grow by soil depth because of the effect this has on soil moisture, favouring *M. uniflora* in deeper soil that holds more soil moisture and *S. smallii* in shallow, drier soil.	(Sharitz & McCormick 1973)
11	limestone grassland	Derbyshire, UK	1, 300	25 species of grass and forb	13 species segregated on gradients of soil depth and 9 migrated along these in response to experimental watering and drought treatments.	(Fridley *et al.* 2011)

881

882 **Table 2**

883 Table 2. Studies of hydrological niche segregation through different strategies of water acquisition such as different phenologies or different

884 rooting depths. Any differences among species are those found to be statistically significant in the original studies

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
12	Dry desert	Namibia	12	3 common trees *Acacia erioloba, Tamarix usneoides* and *Faidherbia albida*	Stable isotopes were used to partition water sources between fog, ground water, and soil depths 0 - 1m or 1.5 - 3.0m depth. None used fog water. For adult trees in the dry season, > 50% was obtained from deep soil in *A. erioloba* & *T. usneoides*, but the spp. accessed different amounts from shallow soil (6% & 17%). *F. albidia* used mainly ground water (52%) and deep water (30%).	(Schachtschneider & February 2010)
13	Desert	Utah, USA	119	5 annuals, 7 herbaceous perennials, 13 woody perennials	Stable isotope analysis indicated that there was no difference among life forms in their exploitation of different water sources in spring, but that differences did	(Ehleringer *et al.* 1991; Lin *et al.* 1996)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				and a succulent perennial	occur both within and between life forms in summer. Experimental rainfall additions in summer confirmed that species exploit this water source to different degrees.	
14	Desert	California, USA	144	Co-dominant shrubs *Haplopappus cooperi* and *Chrysothamnus teretifolius*	Species had different rooting depths. Experimental removal of *C. teretifolius* (rooting depth 40cm) improved the water status (Ψ) of *H. cooperi* (rooting depth 20cm), but not vice-versa.	(Manning & Barbour 1988)
15	Intermountain desert basin	Colorado, USA	178	Grasses: *Sporobolus airoides* and *Distichlis spicata*; shrubs: *Sarcobatus vermiculatus* and *Ericameria nauseosa*	Experimental rainfall treatments and stable isotope analysis demonstrated that the grasses used surface water while the shrubs used ground and surface water. The shrubs differed from each other in their response to variation in surface water availability.	(Kray *et al.* 2012)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
16	Savanna	Arizona, USA	202	A dominant tree *Quercus emoryi* and a co-ocurring dominant C-4 grass *Trachypogon montufari*	Stable isotope analysis demonstrated that established trees and grass utilized different water sources. However, 2 month old tree seedlings obtained water from above the zone exploited by the grass, competed in the same depth zone at ages 1 and 2, and then penetrated to deeper soil when older.	(Weltzin & McPherson 1997)
17	Pinyon- Juniper woodland	Utah, USA	232	*Pinus edulis* and *Juniperus osteosperma*	Sap flux and stable isotopes were used to determine the relative use of water by the two species in the two zones 5 - 45cm and > 45cm soil depth. *P. edulis* depended on summer rain near the surface while *J. osteosperma* did not. At other times of year the species had similar water utilization to each other.	(West *et al.* 2007)
18	Woodland	Utah, USA	319	2 trees *Juniperus osteosperma* & *Pinus edulis* & 2 shrubs *Artemisia*	Stable isotope analysis indicated that *C. nauseosus* depended on ground water while the other 3 species used both precipitation and groundwater, but to	(Flanagan *et al.* 1992)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				tridentate & *Chrysothamnus nauseousus*	varying degrees.	
19	Shortgrass steppe	Colorado, USA	321	A C-4 grass *Bouteloua gracilis,* a shrub *Atriplex canescens,* and a tree *Populus sargentii*	Stable isotopes indicated that *P. sargentii* depended exclusively on ground water during the growing season, while *B. gracilis* depended exclusively on rainfall from near the soil surface. *A. canescens* probably used both sources, but mainly rainfall obtained from deeper soil. The effects of experimental removal, separately and in combination, of the grasses & shrubs increased soil water content in different soil layers in a manner consistent with the species' patterns of utilization.	(Dodd *et al.* 1998)
20	Steppe	Inner Mongolia, China	341	C-3 Grasses: *Stipa grandis*, *Agropyron cristatum*, *Leymus chinensis*; C-4 grass: *Cleistogenes*	Stable isotopes showed that the shrub *Caragama microphylla* used only deep soil water, the C4 grass *Cleistogenes squarrosa* used only summer rainfall, and the C3 grass species used both sources of	(Yang *et al.* 2011)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				squarrosa; shrub: *Caragama microphylla*.	water according to availability.	
21	Mediterranean grassland	Greece	364	Two C-3 grasses *Poa bulbosa* and *Anthoxanthum odoratum*, two C-4 grasses *Chrysopogon gryllus* and *Cynodon dactylon*, and the C-3 forb *Rumex acetosella*.	Biomass production was shown to be water-limited in all 5 species. Phenology differed between the C-3 grasses that peaked early in the year, the C-4 grasses that grew later and *R. acetosella* that peaked in biomass between the two groups of grasses.	(Mamolos *et al.* 2001)
22	Mediterranean shrubland	Spain	450	Shrubs: pre-Mediterranean *Quercus coccifera, Arbutus unedo, Pistacia lentiscus;* Mediterranean *Erica multiflora,*	Stable isotope analysis indicated differences in use of water sources between species with different evolutionary history (pre-Mediterranean *vs*. Mediterranean) and between some species in the time of day when different sources were exploited.	(Filella & Penuelas 2003)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				Globularia alypum		
23	Tropical	Lana'i, Hawaii	500	2 dominant and 5 other tree species and a stem succulent	Stable isotopes indicated that most species including the two most abundant trees utilized shallow water sources and were drought tolerant, while an evergreen that is dominant in wetter Hawaiian forests and a stem succulent were drought avoiders and used deeper water. Among the subordinate trees using shallow water, one species was separated from other trees by a much larger distance than expected, suggesting competition might influence its spatial distribution.	(Stratton *et al.* 2000)
24	Kwongan	Western Australia	531	3 congeneric shrubs: *Banksia hookeriana, B. attenuata* and *B. menziesii*	Water relations did not differ among the 3 species during the dry season. Shoot phenology and root distributions were also the same.	(Lamont & Bergl 1991)
25	riparian	Kansas, USA	586	3 creekside trees	None of the 3 species showed signs of	(Maricle *et al.*

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
	woodland			*Lonicera tatarica*, *Morus alba* and *Celtis occidentalis*	water stress during soil drying. Stable isotopes indicated that *C. occidentalis* obtained water from a shallower depth than the other two species, even though this species had the deepest roots.	2011)
26	old growth temperate broadleaf forest	northern Thuringia, Germany	590	3 co-dominant trees *Fagus sylvatica*, *Tilia sp.*, *Fraxinus excelsior*	Stable isotopes were used to estimate depth of water sources from the soil profile for species growing in single-species clusters and in 3-spp mixtures. Overlap was greater among single species than in mixtures due to *Fraxinus* altering its source depth in mixture.	(Meissner *et al.* 2012)
27	Experimental grassland	Umeå, Sweden	600	Up to 12 grassland species sown in plots containing 1, 2, 4, 8 or 12 species	Community evapotranspiration and biomass production showed over-yielding in control mixtures compared to monocultures, but this was absent in a drought treatment, suggesting complementary use of soil moisture under normal conditions.	(Verheyen *et al.* 2008)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
28	Alpine meadow	Mt. Balang, China	710	3 herbs *Caltha palustris, Veratrum nigrum, Stellera chamaejasme*	Stable isotopes showed that the 3 species used water from 4 soil depth zones differently.	(Leng *et al.* 2013)
29	sub-alpine	Sichuan, China	711	2 co-dominant shrubs *Quercus aquifolioides* and *Salix luctuosa*	Stable isotopes used to measure use of water from 6 depth horizons in the monsoon month of August. The two species were very similar in their use of water from different depths, both matching relative amounts used to relative amounts of water present in the top 50cm of soil.	(Liu *et al.* 2011)
30	savanna	Texas, USA	720	2 shrubs *Prosopis glandulosa* (overstorey), *Zanthoxylem fagara* (understorey) and up to 8 other woody understorey	Rooting depth profiles were different among the species (especially *P. glandulosa* and *Z. fagara*), but stable isotopes sampled during the season of greatest rainfall (late summer - fall) showed no differences among species in the depth of water sources utilized. Hydraulic lift and recruitment around	(Midwood *et al.* 1998), (Zou *et al.* 2005), (Stokes & Archer 2010)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				species	nurse plants produce positive interactions among species.	
31	Karst savanna	Texas, USA	800	Two dominant evergreen trees *Juniperus ashei* and *Quercus fusiformis*	ψ_p lower in *J. ashei* than *Q. fusiformis*, suggesting that the roots of the former are shallower than those of the latter species. However, stable isotopes of co-occurring trees of the two species showed that both utilized the same water source during drought.	(Schwinning 2008)
32	Tallgrass prairie	Kansas, USA	835	7 species including 3 dominant C-4 grasses and 4 C-3 forbs and shrubs	Stable isotopes and Ψ measurements showed all species used water from surface (0 - 25cm) soil in the wet summer season. In the dry season C-4 grasses continued to used this source, while C-3 species used predominantly deeper water	(Nippert & Knapp 2007a, 2007b)
33	Sub-alpine forest	SW China	884	Dominant tree *Abies faxoniana*, mid-storey tree *Betula utilis* and	Stable isotopes showed that *A. faxoniana* depends throughout the year mainly on ground water, while the other two species depend mainly on rainfall, except when	(Xu *et al.* 2011)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				understory bamboo *Bashania fangiana*	this is scarce.	
34	Seasonally dry forest	Yucatan, Mexico	1, 000	3 evergreen *Brosimum alicastrum, Talisia olivaeformis, Ficus cotinifolia*, 3 deciduous *Cedrela odorata, Spondias purpurea, Enterolobium cyclocarpum* and 1 semi-deciduous *Cordia dodecandra* tree species	Stable isotopes sampled in the peak of the dry season were used to estimate the % water used that was derived from three soil depth zones and from ground water. None of the species used ground water for more than 11% of their supply. 3 species *F. cotinifolia S. purpurea C. dodecandra* used water mainly from the soil surface (0 - 15cm) and the other 3 from deep bedrock (70 - 300cm) *E. cyclocarpum B. alicastrum T. olivaeformis* with differing utilizations of water from the zone between 15 - 70cm.	(Querejeta *et al.* 2007)
35	chaparral	S. California, USA	1,000	4 coexisting shrubs: *Quercus durata, Heteromeles arbutifolia, Adenostoma fasciculatum,*	Water use patterns suggested that *Q. durata* accessed water from a depth of ≥ 2m, *H. arbutifolia* and *A. fasciculatum* from 0.75m and *R. californica* from 0.5m.	(Davis & Mooney 1986)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				Rhamnus californica		
36	savanna	Côte d'Ivoire, W. Africa	1, 210	Shrubs and bunch grasses	Root distributions and stable isotopes indicate that shrubs and grasses both obtain water from near the surface and do not exploit water from substantially different depth zones.	(Leroux *et al.* 1995)
37	Woodland	N. Queensland, Australia	1, 400	4 dominant trees *Corymbia clarksoniana, Lophostemon suaveolens, Eucalyptus platyphylla* and *Melaleuca viridiflora*	Stable isotopes sampled towards the end of the dry season for one individual of each species suggested that *C. clarksoniana* obtained all of its water from ground water, *M. viridiflora* obtained 53–77% from this source and *L. suaveolens* and *E. platyphylla* obtained between 0% and 15% from ground water.	(Cook & O'Grady 2006)
38	Tropical, seasonal rainforest	SW China	1, 487	2 dominant, canopy trees *Pometia tomentosa* and	In the dry season *G. subaequalis* utlized water mainly from shallow soil (< 60cm) and *P. tomentosa* from deeper soil (>	(Liu *et al.* 2010)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				Gironniera subaequalis	60cm). Seedlings of the latter species also acquired significant amounts of water from fog.	
39	Savanna	Brasilia, Brazil	1, 550	5 deciduous and 5 evergreen woody species	Stable isotope analysis during the dry season divided the species into a group of 5 mainly evergreen species that exploited water in the top 170cm of the soil, a group of 4 mainly deciduous species obtaining water from below 250 cm and one deciduous species that was intermediate between the two groups.	(Jackson *et al.* 1999)
40	Seasonal tropical forest	Yucatan, Mexico	1, 650	3 evergreen trees *Coccoloba diversifolia, Esenbeckia pentaphylla, Vitex gaumeri* and 3 drought-deciduous trees *Caesalpinia gaumeri, Lonchocarpus*	In early but not in late successional forest, stable isotopes indicated that the 3 evergreen species accessed deeper water than the 3 deciduous species.	(Hasselquist *et al.* 2010)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
				castilloi, Lysiloma latisiliquum		
41	riparian tropical rainforest	NE Australia	1, 680	Co-dominant canopy species, tree species: *Doryphora aromatica, Argyrodendron trifoliolatum, Castanospora alphandii* and climbing palms *Calamus australis* and *C. caryotoides*	In the dry season, stable isotopes indicated that two of the trees depended on stream water while the other three species drew water from a zone above the water table.	(Drake & Franks 2003)
42	Tropical	Barro Colorado Island nature monument, Panama	2, 600	9 species of deciduous and evergreen broadleaf tree, one palm, one liana, and 5 species of small trees and shrubs	Stable isotope analysis during the dry season indicated a high degree of vertical partitioning of soil water, especially among evergreen trees and shrubs.	(Jackson *et al.* 1995)

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
43	tropical forest	Barro Colorado Island, Panama	2,600	17 spp. of forest trees ranging from evergreen to varying degress of dry season deciduousness	Stable isotope and water use measurements made during the dry season demonstrated that smaller diameter trees sourced deeper water than larger ones. Ability to maintain sap flow during the dry season varied with leaf phenology, with evergreen species tapping increasingly deeper water as the dry season progressed.	(Meinzer *et al.* 1999)

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886

887 **Table 3**

888 Table 3. Studies of hydrological niche segregation in time (temporal storage effect). Any differences among species are those found to be

889 statistically significant in the original studies

#	Vegetation type	Location	Mean precip. (mm/y)	Species	Evidence	Reference
44	Steppe	Patagonia, Argentina	174	6 shrubs *Anarthrophyllum rigidum, Adesmia volckmanni, Berberis heterophylla, Mulinum spinosum, Schinus poligamus* and *Senecio filaginoides*	Species varied greatly in their uptake of an experimentally-applied pulse of rainfall applied at the begining of a dry summer, from 0% use of rainfall to 29%.	(Kowaljow & Fernandez 2011)
45	Desert	Sonoran desert, Arizona, USA	250	10 species of winter annual	Differences among species in how germination and fecundity respond to year-to-year variability in rainfall creates a storage effect that facilitates coexistence. Species' specialization into temporal	(Angert *et al.* 2007, 2009)

					(hydrological) niches is the result of a trade-off between relative growth rate and water use efficiency.	
46	Desert	Chihuahua, Mexico	270	2 shrub species: *Atriplex acanthocarpa* and *A. canescens*	*A. canescens* was more resistant to drought than *A. acanthocarpa*, but this relationship was reversed for growth response to rainfall, suggesting that year-to-year variation in rainfall/ drought could aid coexistence.	(Verhulst *et al.* 2008)
47	Steppe	NW China	380	3 dominant species: perennial grass *Stipa bungeana*, a shrub *Artemisia ordosia*, and a herb *Cynanchum komarovii*	Using stable isotopes, differences among the three species were found in how they utilized water from summer rainfall events of different size.	(Cheng *et al.* 2006)
48	Prairie	Kansas, USA	580	3 dominant perennial grasses (*Bouteloua curtipendula, Bouteloua hirsuta,* and *Schizachyrium scoparium*)	Long-term monitoring of the grasses was used to build models of the response of each population to climate. The models showed that a positive population growth rate at low density depended on climate variability in 2 of the 3 species.	(Adler *et al.* 2006)

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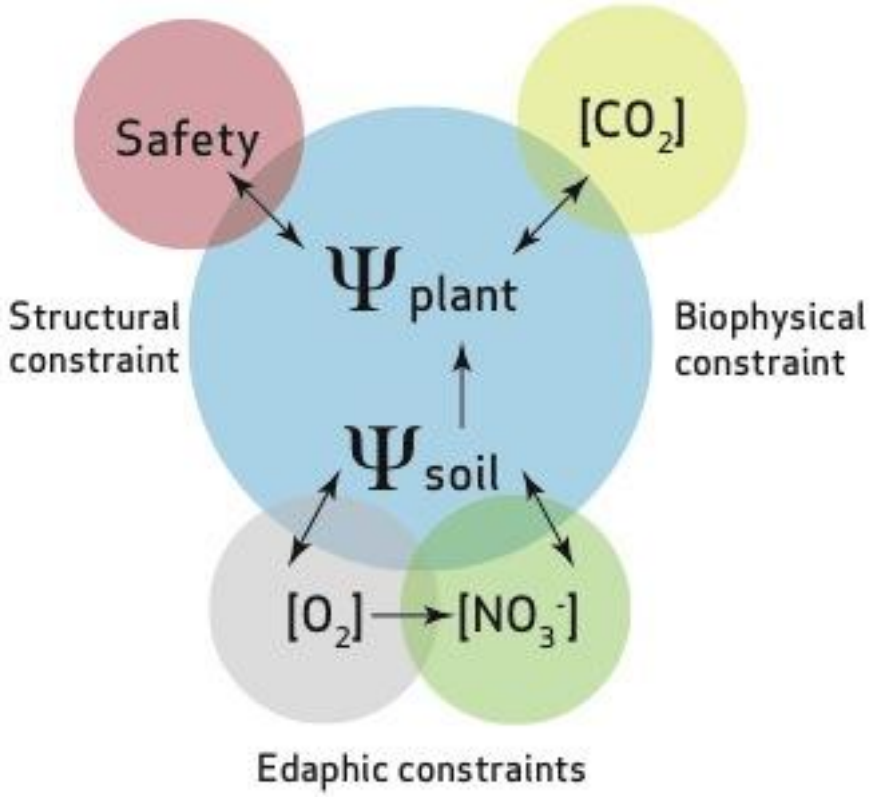
891

Figure legend

Fig.1. A Venn diagram of the relationship between plant (ψ_{plant}) and soil (ψ_{soil}) water potentials and the ability of plants to take up CO_2, O_2, NO_3^- and to resist failure of the vascular system (safety). Double-headed arrows indicate trade-offs and the single-headed arrows indicate the positive relationships between ψ_{plant} and ψ_{soil} and between aerobic conditions and the availability of nitrate in soils.

899 ***Figure***

900 Fig.1.



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